Evolutionary radiation of non-marine molluscs in East Asia.

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論文内容の要旨

Summary

Understanding how phenotypic diversity and diversity patterns have been created is a central subject of evolutionary biology and conservation biology. Non-marine molluscs have been treated as excellent models to investigate causes of morphological evolution, speciation and diversity patterns. East Asia including Japanese Archipelago is known to be a hotspot of land and freshwater snails because of their high species diversity, while there have been few systematic and phylogenetic studies of land and freshwater snails.

In Chapter 2, I documented extensive incongruence between molecular phylogeny and the current taxonomy of the freshwater gastropod family Viviparidae in Japan. A molecular phylogeny for East Asian viviparids comprises three major clades. Among these clades, two are composed of paraphyletic or highly polyphyletic taxonomic species. The observed incongruence between phylogeny and taxonomy may be due to incomplete lineage sorting, introgressive hybridization and/or phenotypic plasticity, suggesting substantial revision is required not only for understanding evolutionary history of these groups but also for developing conservation programs.

In Chapter 3, I reconstructed a molecular phylogeny of the land snail genus *Cyclophorus* using three genes to determine whether their morphological traits and the current taxonomy of the species reflect their phylogenetic relationships. The present results showed that the geographical distributions of the lineages and current taxonomy do not reflect their phylogenetic relationships. In addition, morphological analysis indicated that cryptic species nevertheless shell morphological diversity within species is relatively high in several species. The present study showed that the current zoogeographical boundary lines for animal distribution of the Ryukyu Islands did not reflect evolutionary patterns in *Cyclophorus*. This study suggests that a further taxonomic revision of Japanese *Cyclophorus* is needed for biodiversity conservation.

In Chapter 4, I investigated the molecular phylogeny of the East Asian camaenid land snail genera *Aegista*, *Landouria*, *Trishoplita*, and *Pseudobuliminus* to test whether morphology and current taxonomy reflect phylogenetic relationships. The results documented extensive parallel evolution and substantial incongruence between taxonomy and molecular phylogeny. Many morphological traits were independently gained or lost in a number of lineages. Although genital anatomy reveals phylogenetic conservatism to some extent, love dart and dart-related organs were lost independently. Accordingly, classification of these genera based on morphological traits did not reflect phylogenetic relationships, and, overall, these genera except for a few species should be tentatively assigned to a single genus as *Aegista*. The present findings suggest that radical revision is required for the taxonomy of camaenid land snails.

In Chapter 5, I investigated the relationship between the shell morphology and habitat use of camaenid land snails of the genus *Aegista* and clarify the causes of the divergence in shell morphology among phylogenetically related species. The results showed that arboreal species have evolved independently from ground-dwelling species at multiple times. A significant association was found between shell shape and habitat use despite of the existence of a certain degree of phylogenetic constraint between these traits. The development of a well-balanced shell shape is one effective method for reducing the cost of locomotion under the force of gravity in each life habitat, resulting in the divergence in shell morphology and the independent evolution of morphologically similar species among different lineages. The present study suggests that ecological divergence is probably the cause of shell morphology divergence in land snails.

In Chapter 6, I described *Aegista hiroshifukudai* n. sp. from Yamaguchi Prefecture, the Chugoku District, western Honshu, Japan. The new species is assigned to *Aegista* based on its morphology and molecular phylogeny. *Aegista hiroshifukudai* n. sp. is phylogenetically distinct from all other closely related species and the shell has a relatively taller spire.

In Chapter 7, I investigated the molecular phylogeny of *Bradybaena* and *Phaeohelix*, to clarify whether morphological traits and the current species taxonomy of these genera reflect their phylogenetic relationships. The results showed that they are genetically divided into three clades, and the geographical distribution pattern of the lineages tends to reflect phylogenetic relationships. In addition, passive long distance dispersal by ocean current influenced their evolutionary history. The nominal species taxonomy was not consistent with their molecular phylogenetic relationships. In addition, present findings showed that *Phaeohelix* should be synonymized with *Bradybaena*. This study suggests that a further taxonomic revision of Japanese Camaenidae is needed.

In Chapter 8, I investigated evolutionary history of the all Japanese *Bradybaena* species with particular focus on dispersal patterns and vicariance events in the Ryukyu Islands, using molecular phylogeny. The inferred mitochondrial and nuclear gene trees of *B. c. circulus* of the Ryukyu Islands and *B. p. iheyaensis*, *B. pellucida* and *B. similaris* showed incongruence between morphology and phylogeny. All Japanese species were monophyletic, and they are separated into seven major clades. In addition, the geographical distribution of the clades reflected their phylogenetic relationships but not current taxonomy. Particularly almost all subclades of clade 7 showed relatively wide distribution range. In the present study, it is suggested that both vicariance and long range dispersal play a crucial role in creating biogeographical patterns of *Bradybaena* on the Ryukyu Islands.

論文審査結果の要旨

本研究は、日本を中心とした東アジア地域の陸貝及び淡水貝類について、その遺伝的多様化の歴史を推定するとともに、生態や形態分化のプロセスを解明することを目的として行われたものである。

日本全土および韓国、中国～東南アジアに至るオオベソマイマイ群陸貝の核およびミトコンドリアDNA の分析を行うことにより、従来別属とされるほどの両者の著しい形態上の差異をもつグループが実際には近縁であり、かつ従来形態から同一の属に区分されていた種群が多系統であることを示した。さらにこれらの著しい形態的な平行進化が、樹上性、地上性という生活様式の分化と強く関係していることを明らかにした。これらの知見を通じて、本グループの生態的な分化がその著しい形態的多様化の要因であることを示した。本研究は、生活様式の分化が近縁種間に形態的な分化を引き起こしたことを示す非常に有力な証拠であり、進化生物学的に重要な発見であると言える。

次に琉球列島の陸貝（オナジマイマイ群およびヤマタニシ群）について、核およびミトコンドリアDNA の分析を行うことにより、その進化史と遺伝的多様性の生物地理パターンの形成プロセスを解明した。従来、琉球列島の動物相については、地史的な分布の分断が多様化の主因と考えられていたのに対し、本研究の結果から、長距離の受動的分散が、地理的隔離や生物地理パターンの形成に重要な役割を果たしていることを示した。

さらに日本及び中国、韓国のタニシ科淡水貝類の遺伝的多様性の解析を行い、その進化史と生物地理パターンの形成過程を推定した。その結果、日本の淡水域に最も多産しかつ広域に分布するヒメタニシは、ごく最近人為的に中国からもたらされた帰化種であること、一方マルタニシは中国の個体群とは遺伝的に大きく異なる別種であること、また琵琶湖固有属とされてきたナガタニシは、遺伝的にはオオタニシと区別できないほど近縁であることを示すなど、従来の日本の淡水貝類相に関する常識を覆す知見を得た。

以上の成果は５編の論文として海外学術誌に筆頭著者として公表済みである。これらは平野君が主体となり、計画の立案から実施まで独自のアイデアをもとに取り組んだ成果である。このことは平野君が、自立して研究活動を行うに必要な高度の研究能力と学識を有することを示している。従って平野尚浩君提出の論文は，博士（生命科学）の博士論文として合格と認める。